# When Do Shifts in Trait Dynamics Precede Population Declines?

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ABSTRACT: Predicting population responses to environmental change is an ongoing challenge in ecology. Studies investigating the links between fitness-related phenotypic traits and demography have shown that trait dynamic responses to environmental change can sometimes precede population dynamic responses and thus can be used as an early warning signal. However, it is still unknown under which ecological and evolutionary circumstances shifts in fitness-related traits can precede population responses to environmental perturbation. Here, we take a trait-based demographic approach and investigate both trait and population dynamics in a density-regulated population in response to a gradual change in the environment. We explore the ecological and evolutionary constraints under which shifts in fitness-related traits precede a decline in population size. We show both analytically and with experimental data that under medium to slow rates of environmental change, shifts in a trait value can precede population decline. We further show the positive influence of environmental predictability, net reproductive rate, plasticity, and genetic variation on shifts in trait dynamics preceding potential population declines. These results still hold under nonconstant genetic variation and environmental stochasticity. Our study highlights ecological and evolutionary circumstances under which a fitness-related trait can be used as an early warning signal of an impending population decline.

*Keywords:* population decline, quantitative trait, early warning signals, demography.

## Introduction

Exogenous pressure can force complex systems with alternative stable states toward so-called tipping points, the point at which the system's state can rapidly and substantially change in response to a small perturbation (May 1977; Sousa 1984; Hutchings and Reynolds 2004; Frank et al. 2011). Examples of such transitions are documented from rapid shifts in shrub cover in grasslands (Kéfi et al. 2007) to the collapse of fisheries (Jackson et al. 2001; Frank et al. 2011), and have been shown to be experimentally inducible in laboratory systems (Drake and Griffen 2010; Dai et al. 2012, 2013). The nonlinear nature of such transitions makes them difficult to predict but may be possible through the identification of statistical signals embedded in time series data, typically termed early warning signals (EWSs; Wissel 1984; Dakos et al. 2008; Scheffer et al. 2009). Such statistical signals arise from a system's behavior before a critical transition (van Nes and Scheffer 2007; Scheffer et al. 2012), whereby it takes longer to return to its original equilibrium state after every perturbation. This behavior of the system is known as critical slowing down.

Critical slowing down behavior is predicted to lead to increasing variance and autocorrelation in the abundance time series in the region of a bifurcation. However, shifts in variance or autocorrelation in the abundance time series might not be the only indicators of whether a population is nearing a tipping point (Clements and Ozgul 2016). External environmental change has been shown to substantially affect phenotypic trait distributions along with changes in demography (Traill et al. 2014; Pigeon et al. 2017). Phenotypic traits—for example, body size—are intimately linked with an individual's survival and reproductive success (McNamara and Houston 2008), vulnerability of a population to extinction, and fluctuations in population size (Olden et al. 2007; van Benthem et al. 2017). Changes in body size have also been shown to influence resilience of food webs to disturbance (Woodward et al. 2005). Furthermore, recent work has also suggested body size as a measure of stability, as shifts in body size of diatoms were detected before a regime shift in a lake ecosystem (Spanbauer et al. 2016). Thus, tracking shifts in such fitness-related phenotypic trait values might allow us to infer how stable the population is, which can inform us about an impending population decline.

Empirical observations from experiments and natural populations have shown that including information from phenotypic traits such as body size into abundance-based stability indicators improves the accuracy of predictions of population collapse (Clements and Ozgul 2016; Clements et al. 2017), but the circumstances under which doing so is informative is still unknown. The response of a population to a change in the environment can be a combination of ecological and evolution-

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ary responses governed by factors such as genetic variation or adaptive plasticity (Charmantier et al. 2008; Ozgul et al. 2012). Plastic responses to a change in the environment can be fast, and such responses have been shown to stabilize population dynamics (Charmantier et al. 2008; Reed et al. 2010). However, if the environment keeps on changing, a population might deplete its plastic capacity and standing genetic variation, causing it to eventually decline. This decline in population size will also be dependent on the reproductive rate, that is, whether a population is growing faster or slower (Hutchings et al. 2012; Juan-Jordá et al. 2015). In addition, because of directional change in the environment, selection will act on the standing genetic variation of that trait, and the higher the genetic variation in the trait, the faster will be the evolutionary response (assuming the trait is heritable; Sanchez and Gore 2013; Cortez 2016). Such theoretical expectations raise important practical questions: Can a shift in phenotypic trait dynamics occur before an eventual decline in population size and before shifts in EWSs? Under what circumstances is this possible? If such a shift in trait dynamics occurs, what are the factors that govern the earlier occurrence of this shift?

To answer these questions, we used a combination of theoretical and experimental approaches to understand the circumstances under which information from trait values can be useful to predict a potential population decline. First, we integrated quantitative genetics and population dynamics in a theoretical approach and showed both analytically and numerically whether and under what circumstances shifts in trait dynamics can precede population declines. We then qualitatively test our predictions using microcosm data where replicate protist populations were forced to collapse under different environmental perturbations (Clements and Ozgul 2016). Finally, we evaluate through numerical simulations how genetic variation, adaptive plasticity, and reproductive rate affect when shifts in trait dynamics precede decline in population size and shifts in EWSs.

## Methods and Modeling Framework

### *The Model*

In our model, we consider a closed population that has nonoverlapping generations and is subjected to density-dependent population regulation. We assume in our population that all individuals experience the same environment; that is, there is no spatial heterogeneity. Fitness of individuals in the population is determined by a quantitative trait $z$ that is under stabilizing selection. Under these assumptions the dynamics of the population and the mean value of the trait can be written as

$$N_{t+1} = N_t \overline{R}_t = N_t R_0^{\left(1-\frac{f(N_t)}{f(K)}\right)} \overline{W}, \tag{1}$$

$$\bar{z}_{t+1} = \bar{a}_t + \sigma_a^2 \frac{\partial \ln \overline{W}}{\partial \bar{a}} + bu_t \tag{2}$$

(Gomulkiewicz and Holt 1995; Chevin and Lande 2010). Equation (1) describes the dynamics of a population, and equation (2) describes the dynamics of average trait value $\bar{z}$ due to changes in the mean fitness $\overline{W}$ caused by changes in the selecting environment $E_t$. The term $\overline{R}_t$ is the average growth rate of the population at generation $t$, and $R_0$ is the net reproductive rate. The exponent $1 - f(N_t)/f(K)$ captures the density dependence in the population. The average fitness of the population is quantified by the term $\overline{W}$. The term $\bar{z}_{t+1}$ in equation (2) is the mean value of the trait at generation $t + 1$, and $\bar{a}_t$ is the mean breeding value of the population at generation $t$. The additive genetic variance in the mean trait is quantified by $\sigma_a^2$ in equation (2), and $\partial \ln \overline{W}/\partial \bar{a}$ is the gradient of selection on the mean trait $\bar{z}$. The term $bu_t$ quantifies the average plastic response of the trait, where $b$ is the strength in plasticity and $u_t$ is the environmental cue (see table 1).

The term $\overline{W}$ in equation (1) can be expanded as

$$\overline{W} = \int W(z,\theta)p(z)dz = \frac{w_z}{\sqrt{w_z^2 + \sigma_z^2}} \exp\left(-\frac{(\bar{z}_t - \theta_t)^2}{2(\sigma_z^2 + w_z^2)}\right), \tag{3}$$

where the integral $\int W(z,\theta)p(z)dz$ is over all trait values in the population and gives the average fitness due to the trait $z$. The term $W(z,\theta)$ is the Gaussian stabilizing fitness function given as $W(z,\theta) = \exp(-(z-\theta)^2/2w_z^2)$, with width $w_z^2$ and optimum phenotype of $\theta$. Hence, an individual's fitness will thus be determined by how far its trait $z$ is from the optimum phenotype $\theta$.

The response of the primary trait $z$ to the environment is modeled using linear reaction norms (Gavrilets and Scheiner 1993). The phenotype of an individual at any generation $t$ in the population is given by

$$z_i = a_i + bu, \tag{4}$$

where $a$ is the breeding value of the individual $i$, which is normally distributed with mean $\bar{a}$ and additive genetic variance of $\sigma_a^2$. Variance of the phenotype $z$ is thus $\sigma_z^2 = \sigma_a^2$. The slope $b$ in our model determines how plastic the trait is and is modeled as a constant value, meaning that plasticity in the trait cannot evolve. The environment in our model determines the optimal phenotypic value $\theta$ for the primary phenotype $z$ and also cues the plastic response. The term $\theta$ is assumed to be linearly dependent on the environment $E$ that selects for a particular phenotypic value such that at any time $t$, $\theta_t = BE_t$. The environmental cue $u$ quantifies how an individual on average perceives the environment. For example, snow cover could be one of the environmental cues for ground

**Table 1:** Variables and parameter values used in the model

| Parameter/variable | Description | Value |
|---|---|---|
| $N_t$ | Abundance of population at time $t$ | Variable |
| $\overline{z_t}$, $\bar{a}_t$ | Mean trait value at time $t$; mean breeding value at time $t$ | Variable |
| $\sigma_z^2$, $\sigma_a^2$ | Variance of mean trait; additive genetic variance or variance of mean breeding value | .05, .1, .2, .3, .4, .5, .6; .05, .1, .2, .3, .4, .5, .6 |
| $b$ | Strength in phenotypic plasticity | .05, .1, .2,.3,.4, .5 |
| $R_0$ | Net reproductive rate | 1.1, 1.15, 1.2, 1.25, 1.3,1.35, 1.5 |
| $u_t$ | Environmental cue at time $t$ | Scenario 1 (high predictability): $-\frac{B}{2}+\frac{B}{2}\exp\left(-\left(\frac{t}{500}C+C\right)\right)$, where $C = 4$; scenario 2 (low predictability): $-.0001$ |
| $\theta_t$ | Optimum trait at time $t$ | Variable |
| $w_z^2$ | Width of Gaussian stabilizing fitness function; measure of strength in selection | 40 |
| $z_i$, $a_i$ | Trait value for an individual $i$; breeding value for an individual $i$ | Variable |
| $E_t$ | External environmental value at time $t$ | Variable |
| $B$ | Coefficient that captures strength in external environmental change | 2 |
| $C$ | Parameter that controls rate of change in external environment $E_t$ | Various: 10.5–120.5 |

Note: Variables are not given any value, but parameters for which the model simulations are tested are given values.

squirrels to come out of their hibernation that correlates with resource availability, the environmental factor (Lane et al. 2012). This means that the cue $u_t$ and the selecting environment $E_t$ are related (Charmantier et al. 2008; Reed et al. 2010). We model this relation by making the environmental cue a function of the selecting environment such that $u_t = f(E_t)$. In the case when $u_t$ is a linear function of the selecting environment $E_t$, changes in the selecting environment trigger a change in the cue response. If $u_t$ is modeled as a constant value and is independent of the selecting environment $E_t$, then changes in the cue will not be correlated to that of the selecting environment. In this case, individuals in the population will not be able to perceive changes in the selecting environment.

In our model we specifically address questions linked with the decline phase of the population and not evolutionary rescue. Evolutionary rescue is a long-term process, which occurs when genetic evolution rescues a population from extinction in response to changes in the environment. Whether this rescue happens will depend on the initial decline phase of the population, as the population might collapse before it can adapt to changing environmental conditions (Gonzalez et al. 2013). Hence, predicting this initial decline phase is of foremost importance if one has to mitigate the demographic response of the population before evolutionary rescue takes place at a later phase.

### *Analytical Framework*

Optimal phenotypic change in our analyses is directional and given by

$$\theta_t = \begin{cases} B, & t < t_{500}, \\ BE_t = Be^{-[(t/500)C+C]}, & t \geq t_{500}, \end{cases} \tag{5}$$

where $B = 2$, $E_t = \exp(-[(t/500)C + C])$, $t$ is the time in generations, and $C$ is a parameter that controls how fast the optimal phenotype changes over time. We vary $C$ over a range of values to create a gradient of environmental change from fast to slow. Without loss of generality, we consider that the average trait value is at its optimum; that is, $\overline{z} = \theta_0 = B$ before the environment shifts at $t = 500$.

Following an environmental change scenario, shifts in trait and population dynamics are calculated by $(\overline{z_0} - \overline{z_t})/\overline{z_0}$ and $(N_0 - N_t)/N_0$, respectively, where $\overline{z_0}$ is the initial average trait value and $\overline{z_t}$ is the average trait value after the optimum phenotype shifts. The term $N_0$ is the abundance at carrying capacity, and $N_t$ is the abundance after the environment shifts. We also consider the analytical cases without the effect of plasticity; that is, $b = 0$ (for plasticity effect, see app. B; apps. A–C, S1–S5 are available online). Hence, all the individuals in the population differ only in terms of their breeding value. For analytical simplicity, we show two very simplistic cases of one-generation change in trait and the population after the opti-

mum environment shifts: case 1, the environmental change scenario that causes $(\overline{z_0} - \overline{z_1})/\overline{z_0} > (N_0 - N_1)/N_0$, that is, shift in trait value before population decline; and case 2, the environmental change scenario that causes $(\overline{z_0} - \overline{z_1})/\overline{z_0} < (N_0 - N_1)/N_0$, that is, shift in trait value after a population decline. We consider in these cases two extreme ends of environmental change: abrupt, large shift in one generation and slow, small shift in one generation. In the case of abrupt and large shift in the environment, the optimum phenotype is allowed to shift in one generation by a large magnitude to a new value of $\theta_1 = 0.5$ from a value of $\theta_0 = 2$ such that $\delta = \theta_0 - \theta_1 = \bar{z} - \theta_1 = 1.5$. Specifically, $\delta$ can be termed as the initial phenotypic lag of the mean trait to the optimum phenotype in one generation. The level of this lag is dependent on how fast the optimum phenotype shifts. A shift of $\delta \geq 1.5$, or a lag of 1.5 in just one generation, causes a substantial population decline (fig. 1). Moreover, such a jump in the optimum phenotype to a new value introduces a novel optimum that is beyond the distribution of the adapted trait distribution (with $\sigma_a^2 = 0.5$). In the case of slow and small shift in the environment, the optimum phenotype in one generation is allowed to shift by a very small amount, $\delta \leq 0.2$. This value corresponds to a shift in the optimum that is not novel and within the realms of the adapted trait distribution. We discuss the analytical results of cases 1 and 2 in "Results."

### *Numerical Simulations*

We performed deterministic numerical simulations of the model described above. We also did stochastic numerical simulations of the model (details in app. C). Dynamics of the trait, population, and optimum environment were iteratively updated using equations (1)–(5). We used the Gompertz density function as the form of density dependence in our model simulations (Gompertz 1825; Chevin and Lande 2010). Without loss of generality, we assumed that the mean trait value is at its optimum $\overline{z_0} = \theta = B$ at the start of each simulation. Environmental change was introduced at $t = 500$ after the population reached its carrying. By varying the parameter $C$ (eq. [5]), we simulated a range of environmental change scenarios from very slow ($C = 10.5$) to fast ($C = 120.5$). In all of our simulations of different rates of environmental change, the optimum environment switched to a new value at $t = 500$. The magnitude of this switch, however, depended on $C$ (eq. [5]). For example, if $C = 20.5$, the optimum took ~30 generations to switch by a magnitude of 1.5 units, and if $C = 120.5$, the optimum took approximately five generations to switch. Next, to quantify whether the trait or population abundance shifted first when the environmental conditions changed, we calculated the area under the curve (AUC) of both the trait shift $(\overline{z_0} - \overline{z_t})/\overline{z_0}$ and the population shift $(N_0 - N_t)/N_0$ over 25 generations after the optimum environment changed. One-generation change was used only in the two extreme cases to elucidate the mathematical simplicity behind the environmental change scenario under which trait could shift before a potential population decline. The AUC, on the other hand, was used to graphically extend the analytical results of one-generation change to 25-generation change. AUC quantified both the magnitude and the timing of standardized

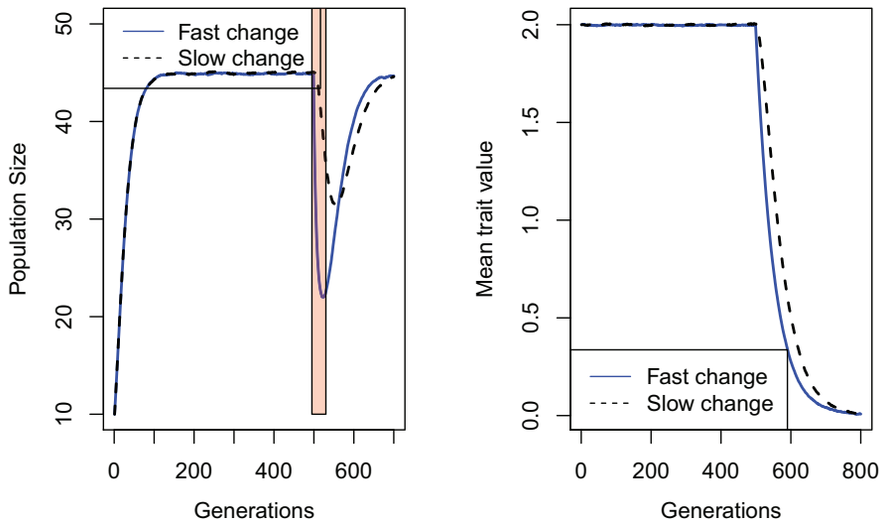


**Figure 1:** Population and trait dynamics under two different environmental scenarios. *Left*, population size declines by ~50%, when the optimum environment shifts fast ($C = 120.5$; solid line), whereas during slow change ($C = 10.5$; dashed line) population declines but to a lesser extent. *Right*, trait dynamics during fast (solid line; $C = 120.5$) and slow (dashed line; $C = 10.5$) environmental change. Data based on deterministic simulations of the theoretical model. Parameters: $\sigma_a^2 = 0.5$, $R_0 = 1.2$, $b = 0.2$, $w_z^2 = 40$.

shifts. With this, we then calculated the metric, Δshift = (AUC of shift in mean value of the trait – AUC of population abundance shift). If Δshift were negative, for a particular rate of change in the environment, it indicated that the population shift was larger and hence the population declined/shifted earlier than a shift in the mean trait value; if Δshift were positive, it meant a shift in the trait value occurred before a decline/shift in population size. We then compared the size of Δshift across rates of change in the environment (for stochastic change in the environment, see app. C). This allowed us to quantify under what environmental change scenarios (from slow to fast) we could expect shift in average trait value to occur before a potential population decline. We then evaluated how the metric Δshift for the range of environmental change scenarios was affected by factors such as genetic variation, strength in plasticity, reproductive rate, and environmental predictability.

### *Rate of Environmental Change*

We varied the parameter $C$ from a value of 10.5 to 120.5 with a step size of 2 to simulate a gradient of perturbations from slow to fast environmental change. We then calculated from equation (5) the time in generations the optimum took to shift by a magnitude of ~1.5 units. This ~1.5 unit of change in the optimum in five generations (when $C = 120.5$) or in more than ~30 generations (values of $C \leq 30$) was enough to cause a significant population decline (fig. 1). We then assessed how Δshift was affected by the rate of environmental change.

### *Environmental Predictability*

We simulated two specific scenarios: (1) when the cue was a linear function of the optimum environment, and hence individuals of the population could perfectly predict changes in the optimum environment; and (2) when the cue was a constant value, and hence individuals had zero predictability of changes in the optimum environment. We then assessed how these two scenarios of environmental predictability affected Δshift. The results of environmental predictability in our model apply when a population has the plastic ability to respond to different environmental conditions (i.e., when $b \neq 0$).

### *Genetic Variation, Strength of Adaptive Plasticity, and Average Reproductive Rate*

We ran a range of numerical simulations with different levels of genetic variation (low to high; $\sigma_a^2 = 0.05, 0.1, 0.2, 0.3, 0.4, 0.5$), low to high strength of adaptive plasticity ($b = 0.05, 0.1, 0.2, 0.3, 0.4, 0.45$), and low to high net reproductive rate ($R_0 = 1.1, 1.15, 1.2, 1.25, 1.3, 1.35, 1.5$). While varying levels of genetic variation from low to high, we kept adaptive plasticity strength at $b = 0.2$ and $R_0$ at 1.2. While varying levels of $b$, we kept $\sigma_a^2$ at 0.5 and $R_0$ at 1.2. Finally, while varying $R_0$, we kept $\sigma_a^2$ and $b$ at 0.5 and 0.2, respectively. For a range of environmental change scenarios, we then evaluated the effect of each parameter value on Δshift.

### *Stochasticity in Optimum Phenotypic Change*

All of the simulations and calculations of Δshift were deterministic. However, any recorded environmental parameter in nature always fluctuates around a mean expectation over time (García Molinos and Donohue 2011). We thus wanted to assess whether adding stochasticity to the changes in the optimum affected our deterministic simulation results. We redid the numerical simulations of the theoretical model but added stochasticity in the optimum phenotypic change (for stochasticity in the growth rate $\overline{R}$, see app. S5). For details, see appendix C. We then assessed how Δshift performed under stochasticity in optimum phenotypic change and how the abovementioned factors affected Δshift.

### *Changing Genetic Variance*

All of the simulations were done assuming that genetic variation remained constant. This is true when a quantitative genetic trait was assumed to be controlled by an infinite number of loci (Falconer and Mackay 1996). Here, we took into account the decreases in genetic variation that might occur because of directional change of the optimum phenotype. For an asexually reproducing population, the variance of the distribution of the breeding values was given by

$$\Delta\sigma_a^2 = -\left(\frac{\sigma_a^4}{\sigma_a^2 + w_z^2}\right) \tag{6}$$

(Bürger 2000). We used numerical iteration to solve the change in genetic variation over time using equation (6). We varied the levels of plasticity, reproductive rate, starting genetic variation, and environmental predictability and calculated Δshift as before (app. S1).

### *Early Warning Signals (EWSs)*

We evaluated how shifts in EWSs compared with shifts in mean trait in response to environmental change for two types of models displaying contrasting bifurcations: transcritical noncatastrophic and fold catastrophic (app. S3). A noncatastrophic transcritical bifurcation occurs when a dynamical system (e.g., a population) moves smoothly from its stable state to an unstable state typified by the extinction point in response to environmental forcing. They are observed in populations with negative density dependence. For this model, we estimated standard deviation and autocorrelation at first lag from abundance data as two main EWSs. Following this, shifts in EWSs and in mean trait were

compared by calculating a metric called $\Delta\text{shift}_{\text{ews}}$ (apps. S3.4–S4). Similar to $\Delta$shift, $\Delta\text{shift}_{\text{ews}} > 0$ would indicate a shift in trait value preceding a shift in an EWS indicator, and $\Delta\text{shift}_{\text{ews}} < 0$ would indicate otherwise. We evaluated $\Delta\text{shift}_{\text{ews}}$ for different levels of plasticity, genetic variation, and reproductive rate. Next, we modified our model to allow for catastrophic fold bifurcation by introducing positive density dependence or an Allee threshold at equation (1) (apps. S3, S4; Luque et al. 2016; Berec et al. 2018). In contrast to transcritical bifurcation, a catastrophic fold transition occurs when a population shifts abruptly from a stable to an unstable state (extinction point) after a small change in the external environment (Dai et al. 2012). For this fold bifurcation model, we evaluated $\Delta\text{shift}_{\text{ews}}$ (see apps. S3, S4). A population near its Allee threshold is always at risk of collapse. A small change in the environmental condition could lead to an abrupt free fall toward local extinction. Because of this reason, once a population crosses this threshold, recovery to its initial state becomes difficult, even after reversing the environmental conditions. Contrastingly, such abruptness is not observed in populations with negative density dependence (or with transcritical bifurcation). In this case, it is possible for a population to recover to its initial stable state on reversing the environmental conditions. Recovery of such populations displaying contrasting dynamics due to differences in the form of density dependence hinges on the fact that population decline is predictable either with the help of EWSs or with shifts in mean traits. Our model (eq. [1]) displays noncatastrophic transcritical bifurcation, which is not representative of a wider class of transitions that could be observed. Hence, we evaluated another type of transition that is abrupt and catastrophic (fold bifurcation model). EWSs are theorized to precede such transitions whether they are abrupt or smooth (Kéfi et al. 2013). However, whether trait shifts could occur before a shift in EWSs still remains a question. Evaluating $\Delta\text{shift}_{\text{ews}}$ for both models would help fill this gap.

### *Experimental Data*

In addition, we analyzed an experimental data where microcosm populations were forced to collapse by varying the rate of decline in food availability (Clements and Ozgul 2016). Clements and Ozgul (2016) used replicate populations of protozoan ciliate *Didinium nasutum* that fed on *Paramecium caudatum*. In the experiment, four different treatments of rates of decline of prey availability were chosen: (1) fast, (2) medium, (3) slow, and (4) a constant prey availability as the control treatment. A total of 60 replicate populations (15 per treatment) were used for the experiment. In our study, we used data only from the deteriorating environment treatments (i.e., fast, medium, and slow decline in prey availability). We analyzed each population's abundance and mean body size time series independently. We then calculated AUC and $\Delta$shift to qualitatively verify our theoretical simulation results (for details, see app. S2).

## Results

### *Analytical Results*

Before a shift in the optimum environment occurs, we assume that the population is perfectly adapted to its optimum phenotype $\theta - \bar{z} = 0$. Considering the starting population size to be at $K$ with no plasticity ($b = 0$), equilibrium population size at any time $t$ from equation (1) is

$$N = \frac{w_z}{\sqrt{w_z^2 + \sigma_z^2}} K$$

(app. A).

*Case 1: Population Declines before a Trait Shift.* Let

$$N_0 = \frac{w_z}{\sqrt{w_z^2 + \sigma_z^2}} K$$

be the population size when the population is at its equilibrium. Next, when the environment changes by a large magnitude in one generation such that $\delta \geq 1.5$, the standardized population shift in one generation is

$$\frac{N_0 - N_1}{N_0} = \frac{N_0 - N_0 \exp\left(-\frac{\delta^2}{2w_z^2 + 2\sigma_z^2}\right)}{N_0} = 1 - \exp\left(-\frac{\delta^2}{2w_z^2 + 2\sigma_z^2}\right) > 0$$

(app. A) and

$$1 - \exp\left(-\frac{\delta^2}{2w_z^2 + 2\sigma_z^2}\right) > \frac{\overline{z_0} - \overline{z_1}}{\overline{z_0}}.$$

*Case 2: Trait Shifts before Population Decline.* When the environment shifts by a small magnitude such that $\delta \leq 0.2$ in one generation, the standardized population shift becomes

$$\frac{N_0 - N_0 \exp\left(-\frac{\delta^2}{2w_z^2 + 2\sigma_z^2}\right)}{N_0} = \frac{N_0 - N_0}{N_0} \approx 0$$

(app. A) because $\exp(-\delta^2/(2w_z^2 + 2\sigma_z^2)) \approx 1$, as $\delta$ is very low, conditional on the fact that $w_z^2 \gg \sigma_z^2$.

In this case, proportional shift in a trait is >0 and hence greater than the population shift (see app. A):

$$\frac{\overline{z_0} - \overline{z_1}}{\overline{z_0}} = \frac{(\theta_1 - \overline{z_0})\left(\frac{w_z \sigma_a^2 \gamma}{\sigma_z^2 + w_z^2}\right)}{\overline{z_0}} > \frac{N_0 - N_t}{N_0} \approx 0.$$

Our two extreme analytical cases showed that if the optimum phenotype shifted by a large magnitude in just one generation, the decline in population size preceded shift in mean trait value immediately. However, this was not true in the scenario when the optimum shifted by a very small magnitude over the course of a single generation. Higher values of plasticity result in larger Δshift, which indicates that the mean trait could shift much earlier than a decline in population size (app. B).

### *Simulation Results*

*Rate of Environmental Change.* Fast changes in the optimum environment caused Δshift to be negative, indicating that population declined before the mean trait could shift. Contrarily, medium to slow changes in the external environment caused Δshift to be positive.

*Environmental Predictability.* When environmental cues are highly predictable, plastic phenotypic responses lead to earlier shifts in mean trait before a decline in population size; that is, Δshift is positive (fig. 2). Low predictability of the optimum environmental change caused Δshift to be negative even when the optimum phenotype shifted by a magnitude of ~1.5 units in more than 15 generations (slow environmental shift; fig. 2).

*Genetic Variation.* Higher genetic variation $\sigma_a^2$ in the trait could lead to earlier shifts in mean trait value. However, such trait shifts could precede population decline only when the optimum environment shifted by a magnitude of 1.5 units in more than 15 generations (slow environmental shift; fig. 3*C*). If the optimum environment shifted to a new value by a magnitude of 1.5 units in less than 15 generations (fast shift), population size always declined before any visible shift in the trait value.

*Adaptive Plasticity.* Given that the environment was highly predictable, strong adaptive plasticity ($b > 0.2$) caused Δshift to be positive (i.e., trait shifted before population decline) even when the optimum shifted fast (magnitude of 1.5 units in <15 generations; fig. 3*B*). However, when phenotypic responses are less plastic ($b < 0.2$), earlier shift in

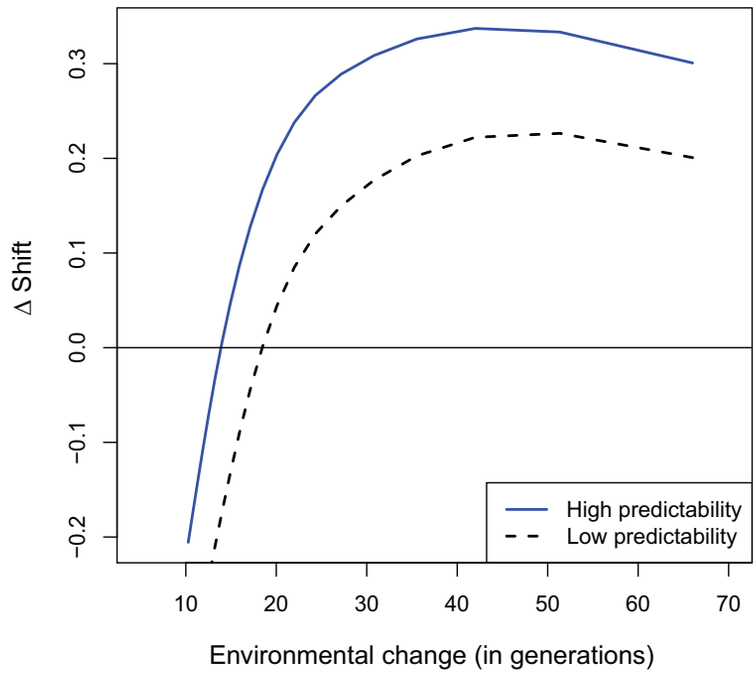


**Figure 2:** Effect of environmental predictability on the magnitude of Δshift; data from numerical simulations of the theoretical model. The Δshift denotes how large and how much earlier the shift occurs in trait dynamics before a decline in the population. If Δshift is positive, shift in average trait value precedes decline in population size and vice versa. The *X*-axis denotes the time in generations it takes for the optimum to change by a magnitude of 1.5 units; hence, 10 on the *X*-axis means the optimum shifts by a magnitude of 1.5 in 10 generations, indicating a fast change, and 60 means the optimum takes 60 generations to shift by a magnitude of 1.5 units, indicating a very slow change. High environmental predictability (blue solid line) facilitates earlier occurrence of trait shift (Δshift being positive) compared with when the environmental predictability is very low (dashed line). The Δshift is always negative (which means population declines precede mean trait shifts) when the optimum environment shifts in ≤15 generations by 1.5 units. Parameters used: $\sigma_a^2 = 0.5$, $R_0 = 1.2$, $b = 0.2$, $w_z^2 = 40$.

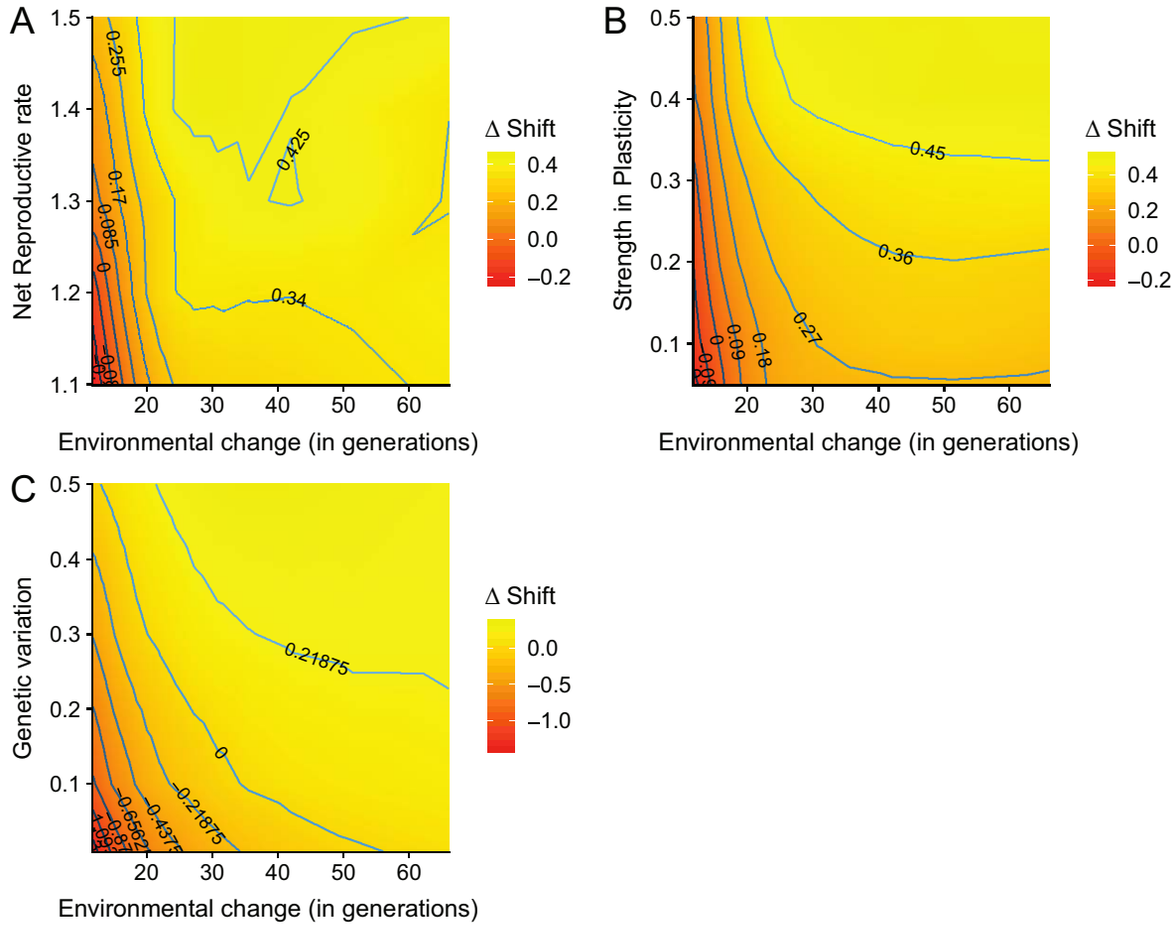


**Figure 3:** Contour plot showing the effect of net reproductive rate, plasticity, and genetic variation on Δshift (contour lines). Shown are the results from numerical simulations of the theoretical model. For a trait shift to be informative of a population decline, the Δshift should always be >0 (contour line = 0). The *X*-axis denotes the time in generations that it takes for the optimum to shift by a magnitude of 1.5 units.

trait value would occur before the population declined only when the optimum environment shifted slowly (>15 generations; fig. 3*B*).

*Reproductive Rate.* For net reproductive rate of 1.2, trait shift occurred earlier than decline in population size; that is, $\Delta\text{shift} > 0$, given the optimum phenotype shifted slowly (by a magnitude of 1.5 units in ~15 generations or more). If the change in the optimum environment is faster than that, a population's net reproductive rate should have to be higher than 1.2 for $\Delta\text{shift} > 0$; hence, shift in the trait value would then be informative of a population decline (fig. 3*A*).

*Stochastic Change in the Optimum Phenotype.* Given that the environment was highly predictable, high genetic variation, high adaptive plasticity in the phenotype, and high net reproductive rate caused Δshift to be positive during stochastic changes in the optimum environment (app. C).

*Evolving Genetic Variation.* When genetic variation in the trait remains constant irrespective of directional selection in the mean trait, Δshift is positive and greater than when there is a directional selection in both the mean trait as well as its genetic variance across medium to slow environmental change (app. S1).

*EWSs and Shift in Mean Trait.* Regardless of an Allee effect (positive density dependence; fold bifurcation model) or negative density dependence (transcritical model) in a population's growth rate, shifts in mean trait could occur before shifts in the two EWSs (fig. S8–S11; figs. C1–C5, S1–S23 are available online). This was particularly evident for medium to slow changes in the environment across the different ecological and evolutionary factors analyzed. Our results thus indicate that shifts in fitness-related traits has the potential to be used as a warning signal of population decline, irrespective of the type of transition.

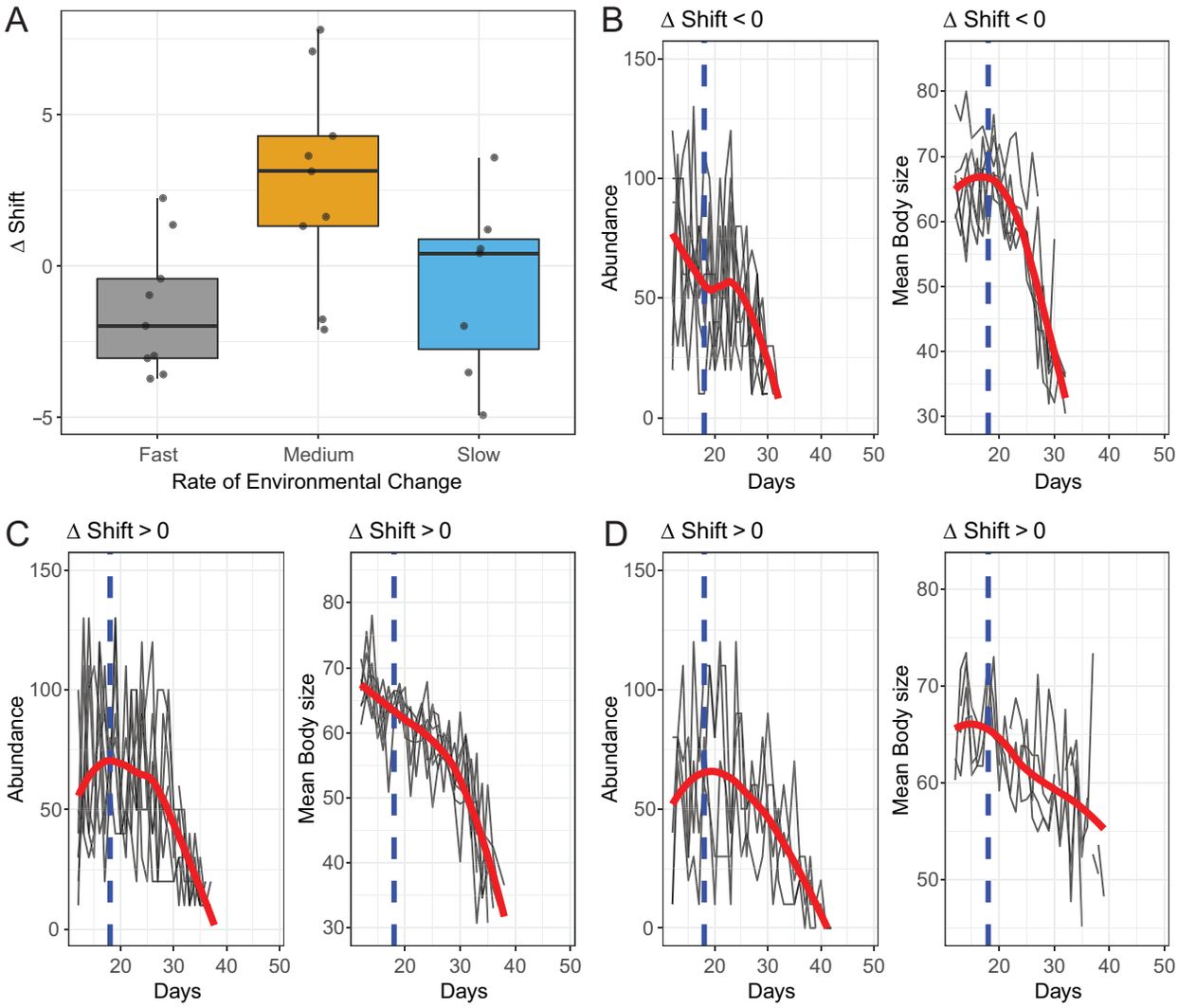


**Figure 4:** Ability of shift in body size dynamics to precede population decline (i.e., $\Delta\text{shift} > 0$) under different environmental regimes for the experimental data from Clements and Ozgul (2016). Note that $\Delta\text{shift} < 0$ if population decline precedes shift in mean body size ($\mu$m) and $\Delta\text{shift} > 0$ if shift in mean body size ($\mu$m) precedes population decline. *A*, $\Delta\text{shift} < 0$ for fast decline in prey availability, indicating that population decline preceded shift in mean body size ($\mu$m). For medium and slow decline in prey availability, $\Delta$shift was largely positive ($\Delta\text{shift} > 0$). *B*, Replicate abundance and body size time series are shown for $\Delta\text{shift} < 0$ (fast decline in prey availability) and for $\Delta\text{shift} > 0$. *C*, *D*, Medium decline and slow decline in prey availability, respectively. Blue dashed line in *B*–*D* indicates the starting point of environmental deterioration. Red solid line indicates loess smoothing across replicates.

*Experimental Results.* Experimental data supported our analytical and simulation results qualitatively. Decline in prey availability from ~300 individuals of *Paramecium caudatum* to 0 happened over a period of 10, 15, and 20 days, indicating three different rates: fast, medium, and slow change in the environment, respectively. Fast change in prey availability resulted in population decline preceding shift in mean body size in seven out of nine replicates (fig. 4*A*). However, shift in average body size preceded decline in population size in seven out of nine replicate populations during the medium rate of prey decline and in four out of seven replicates during the slow decline in prey availability, qualitatively agreeing with our analytical and simulation results.

## Discussion

Recently developed methods have suggested that tracking fitness-related traits might help predict population decline (Clements and Ozgul 2016; Clements et al. 2017). Our analytical and simulation results suggest that when the optimum environment changes relatively slowly, shifts in average trait value may occur earlier than shifts in the population abun-

dance. However, this was affected by the amount of genetic variation, strength in adaptive plasticity, environmental predictability, and speed of life history.

In our simulations, because of high adaptive plasticity ($b > 0.3$), shifts in the average trait value occurred before a decline in population size in response to a fast change in the optimum environment (figs. 3*B*, C2). Such a result was dependent on how predictable the environment was, as plastic response of the trait was mediated by how well the cue was related to a change in the optimum environment. If the cue were correlated with the environment, adaptive plasticity ($b = 0.5$) would cause a shift in average trait value before a decline in population size, even during a significant fast shift in the optimum environment (fig. 3*B*).

While the positive influence of higher genetic variation on population persistence (Willi and Hoffmann 2009) and evolutionary rescue (Hufbauer et al. 2015; Gomulkiewicz et al. 2017) is relatively well studied, little is known about its transient effect on shifts in trait value in response to changes in the environment. Our result suggests that in response to a relatively slow directional change in the environment, high and constant genetic variation in a fitness-related trait will promote faster evolution in the trait value and consequently will cause a faster shift in the average trait value before a decline in population size (figs. 3*C*, C3). In addition, additive genetic variance is also expected to decrease over time because of directional selection acting on the trait (Barton and Keightley 2002). In the results of our simulations where we relaxed the assumption of constant genetic variation, evolutionary change slowed down because of the depletion of genetic variation caused by the directional selection (fig. S1). For this reason, the magnitude of shift in trait value was smaller and slower when compared with another trait shift under the assumption of constant genetic variation for the same scenarios of optimum environmental change (figs. S1–S4). Besides directional selection, a decline in population size can also lead to a decrease in genetic variance (Ashander et al. 2016). Irrespective of the cause, low genetic variance will impede both evolutionary rescue (Hufbauer et al. 2015; Gomulkiewicz et al. 2017) as well as the predictability of population decline with the help of trait information.

Deterministic and stochastic modeling of population persistence in response to a changing environment had earlier revealed the positive effect of reproductive rate on influencing adaptation (Willi and Hoffmann 2009). Earlier studies have also reported that larger species tend to decline in population size more rapidly than smaller species (Olden et al. 2007; Collette et al. 2011) because of differences in life-history strategies and intrinsic growth rates between large and small organisms (Hutchings et al. 2012). Populations of fish with slow life histories (in the family Scombridae) declined faster than those with comparatively faster life histories (Juan-Jordá et al. 2015). Our modeling results reiterated that during a fast shift in the environment, slow-growing populations ($R_0 < 1.2$) would decline before a shift in the trait value could be observed (fig. 3*A*). When we compared two populations with different reproductive rates, the magnitude of Δshift was found to be substantially larger for populations with higher $R_0$ for the same rate of environmental shift (figs. 3*A*, C5) because of the rapid declines of the populations with lower $R_0$.

Our results also suggested that environmental predictability (the correlation between the cue and the optimum environment) was a key determinant in the earlier shift in the trait value in response to a change in the optimum environment. Environmental predictability acted as an interactive factor, determining the speed and magnitude of shifts in trait value, which was driven particularly by the strength in plasticity. Earlier studies had also indicated the positive interactive effects of environmental predictability and adaptive plasticity on population dynamics (Reed et al. 2010; Ashander et al. 2016). Introducing stochasticity in the change in the optimum phenotype (fig. C1) or in the growth rate (app. S5) did not change our results. In the case of stochastic change in the optimum phenotype, environmental predictability was particularly essential as the plastic response of the trait tracked the changes in the optimum, which led to an earlier trait shift before the population declined (figs. 3*B*, C4).

EWSs are shown to exist in models showing both noncatastrophic and catastrophic transitions (Kéfi et al. 2013). In relation to this, our results suggest that regardless of whether our model exhibited noncatastrophic transcritical or catastrophic fold bifurcation, shifts in mean trait value could occur before shifts in EWSs. This was particularly evident for medium to slow change in the optimum environment (figs. S5–S11). Such a shift in mean trait value occurring before EWSs was, however, slightly sensitive to variation in plasticity, genetic variation, and net reproductive rate. Inclusion of stochasticity in optimal environmental change altered the results marginally (figs. S12–S23). Nevertheless, shift in mean trait value in conjunction with shift in EWSs could be used as an indicator of imminent population declines (Clements and Ozgul 2016; Baruah et al. 2018).

Our analytical and simulation results were qualitatively supported by experimental data (fig. 4*A*). In both medium and slow decline in prey availability treatments, shifts in body size occurred before decline in population size. Shifts in body size in response to decline in prey availability that were seen in the experimental data could mostly be attributed to plasticity in body size, as the experimental population was clonal. During fast decline in prey availability, the plastic response of body size over time was not large enough to keep up with the pace of decline in prey availability and hence could not stabilize the loss in fitness. This led to rapid decline in population size before a significant body size shift. However, during medium decline in prey availability, plastic shift in body size

was able to track the decline in prey availability, and as a consequence, a positive growth rate was maintained. However, since the decline in prey availability continued, the plastic capacity of body size was depleted, causing the population to eventually decline, which occurred later than shift in body size. In case of slow decline in prey availability, the change was very slow that led to small plastic shifts in body size before a decline in abundance was seen. These small shifts in body size were not large enough in comparison to decline in abundance, which was reflected in some of the replicates. Shifts in body size thus could be an obvious indicator of environmental deterioration before a response in the population dynamics could be observed. Whether a trait could be considered as an additional indicator of how stressed a population is would depend not only on the identity of the trait but also on the kind of environmental forcing (Clements and Ozgul 2018).

The results presented here were specific to the parameter space but were not restricted to any specific model system (see Chevin et al. 2010). In our model, we made two main assumptions. First, adaptive plasticity in our trait remained constant and hence could not evolve. Studies have observed adaptive phenotypic change without being able to attribute it to genetic change (Ghalambor et al. 2007; Hendry et al. 2008). Our results—under the assumption of constant adaptive plasticity—still held because we explicitly dealt with transient dynamics after the optimum environment shifted. Second, we assumed linear reaction norms. Nonlinear reaction norms are modeled for secondary traits that are components of fitness, but such nonlinear reaction norms can evolve to linear ones in the long term (Gavrilets and Scheiner 1993).

In conclusion, we show that shifts in average trait value could precede shifts in EWSs and population declines in response to a change in the optimum environment, and higher levels of genetic variation, adaptive plasticity, environmental predictability, and reproductive rate strengthened such an earlier shift in the trait value. Using experimental data, we also showed that shifts in average body size could precede declines in population size and hence could be indicative of a future population decline. Such a shift in mean body size preceding a decline in population size was possible if the change in the optimum environment was not fast relative to the generation time of the organism. Thus, shifts in traits may be useful for predicting population collapses in species where life histories are fast, the rate of change of the environment is relatively slow, and the environmental predictability is relatively high, giving hope that methods can be developed for these signals in real world populations.

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